Parasitism ecology of sandalwood (Santalum album L.) for commercial production in the semi-arid tropics

Doddabasawa1,*, B. M. Chittapur2 and R. Lokesh1

1College of Agriculture, Bheemarayanagudi, Yadgir 585 287, India
2Directorate of Extension, University of Agricultural Sciences, Raichur 584 102, India

Successful establishment of a sandalwood plantation is rather difficult due to its complex parasitism ecology and unique silvics of the host species. The present study was therefore undertaken to understand the parasitism ecology of sandalwood under natural population in the semi-arid tropics, covering the northeastern dry zone of Karnataka, India. Sandalwood was found to parasitize on nine different tree species belonging to four families dominated by Leguminosae (six tree species), and the maximum associations occurred with Acacia nilotica. Sandalwood tree requires long-term suitable host not only for mineral nutrients replenishment, but also for water supplementation to maintain plant water potential and minimal composition in above-ground parts apart from sufficient sunlight. Therefore, selection of suitable host assumes significance. A. nilotica and C siamea are preferred hosts, particularly at planting distance of 2.5 m in the semi-arid tropics of India. A planting geometry of 6 m × 6 m or 5 m × 5 m with sandalwood between the host plants at 2.5 to 3.0 m is ideal.

Keywords: Ecology, host species, parasitism, sandalwood, semi-arid tropics.

SANDALWOOD (Santalum album L.) belonging to the family Santalaceae is an evergreen, small to medium-sized hemi-root parasitic tree species endemic to peninsular India1. It is one of the precious and highly valued tree species known for its fragrant heart wood and oil2,3. The oil is extensively used in highly valued perfumery, cosmetics and medicine. Sandalwood also has religious significance and the wood is used in the handicrafts industry4.

India is the major exporter of East Indian sandalwood and accounts for 90% of the total global production. However, production has decreased from 4000 to 500 t/yr in the country, whereas the global demand for sandalwood is between 5000 and 6000 t/yr (ref. 5). This gap has increased the price of sandalwood in the national and international markets by several folds. The decreasing production in India is mainly attributed to factors like illicit felling, forest fires, spike disease, poor natural regeneration, high demand in both national and international markets, and indiscriminate harvesting of trees by uprooting as oil is present in both heart wood and roots6,7.

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1*For correspondence. (e-mail: dkpatil2020@gmail.com)
In order to increase sandalwood production and reduce the pressure on existing natural populations, the Governments of Karnataka and Tamil Nadu have liberalized the policy on growing sandalwood on private lands by amending Forest Act 2001 and 2002 respectively. Further, the fact that it can easily adopt to diverse climatic and edaphic conditions has attracted farmers and corporate to take up sandalwood plantations on a commercial scale.

However, regeneration and establishment of sandalwood plantations have been mostly unsuccessful because of the poor understanding of its parasitism ecology, i.e. sandal–host relationship. Being a hemi-root parasite, sandalwood has unique and complex silvicultural characteristics. Poor understanding of silvics of sandalwood and its parasitism ecology are considered as major constraints in the unsuccessful establishment of plantations. Sandalwood initially requires shade and later abundant light for its growth and development. It coppices well and produces root suckers. However, being a hemi-root parasite, it requires a host for survival, particularly for water and mineral nutrients despite being capable of photosynthesis. Further, it is specific in choosing compatible partners in nature. Sandalwood is a known parasite of more than 300 species from grasses to trees, and even other sandal trees (self-parasitism). Interestingly, differential growth was observed with different hosts, and legumes were preferred over non-leguminous species. However, such studies were mainly restricted to seedling stage and only a few were at field scale under natural conditions. The complexity of process of the parasitism makes it difficult, time-consuming and laborious. Therefore, the present study was conducted under natural ecosystem to understand the nature of parasitism and developmental mechanism in the semi-arid tropics.

The study was carried out at Bheemarayanagudi, Yadgir district, Karnataka, during 2019–20. The climate is semi-arid with short monsoon, mild winter and hot summer. The average annual rainfall is around 750 mm, and minimum and maximum average annual temperatures are 18.6°C to 32.5°C respectively; the mean elevation ranges in translating nitrogen to the fast growing sandalwood. The data collected were subjected to univariate analysis, correlation and one-way ANOVA at a significance level of 0.05. Further, to determine the difference between the means, post-hoc test was performed using Duncan’s test at significance level of 0.05 using SPSS version 20.0.

In this study, sandalwood parasitized nine different tree species belonging to four families. Majority of them belonged to Leguminosae (six tree species), and one each to Meliaceae, Lamiaceae and Arecaceae (Table 1). This shows that sandal prefers leguminous plants for parasitism over non-leguminous plants, as these may help meet its nutrients requirement, especially nitrogen, and other factors such as thin and watery skin roots of Leguminosae family which probably facilitates haustorial connection.

Among the Leguminosae tree species, maximum association was observed with Acacia nilotica (babul; 16), followed by Prosopis juliflora (honey mesquite) whereas lower association was observed with Albizia lebbeck (Indian siris). This indicates parasitism specificity even in the same plant family. Probably host characteristics congenial for parasitism take precedence over other plant characteristics, viz. nodulation, extensive lateral roots, sparse crown, translocation efficiency of mineral nutrients and higher water use efficiency (Table 2). For instance, in several northeastern states in Brazil, roots grow as deep as 53 m and P. juliflora reportedly enriches the soil with organic matter, prevents excessive drying up and supplies the soil with nitrogen by means of Rhizobium fixation, thus giving rise to micro-climate conditions in the area of cactus cultivation. Similarly, A. nilotica species have a long taproot system. As the growth advances, several lateral roots also develop at the end of the first season and subsequently the taproot and lateral roots cannot be easily distinguished. Thus these two form good hosts. However, the lower association of sandalwood parasitism with A. lebbeck might be because most of the atmospheric nitrogen fixed by the genus Albizia used for its own use and nodules formed were few, though bigger in size. Hence, Albizia tree was more frugal in translating nitrogen to the fast growing sandalwood (Table 2).

Sandalwood is a root hemi-parasite and relies on the host for mineral nutrients and water. However, parasitism not only depends on the characteristics of the host, but also on the distance of association from the host. In the present study, significantly longer distance of association was recorded in A. nilotica (2.61 m) followed by Cassia simaea (2.20 m), whereas significantly lower distance of
nodulation and sap flow of xylem tissue. Hence in the aggressive growth, allelo-chemicals released from litter, water use efficiency, lateral root system, sparse crown, sandalwood not only depends on leguminous host, but compared to other species. Lesser growth was observed in association with C. siamea compared to A. nilotica, which could be due to non-nodulation in the former (belongs to family Leguminosae but does not fix atmospheric nitrogen) (Table 2). Our results are in agreement with Xinhua et al., who observed significantly higher net transfer of nitrogen from host plant D. odorifera to hemi-parasite sandalwood under effective nodulation. Similar observations were also made by Subbarao et al., regarding increased nitrogen content in sandal plants grown in association with nodulating Cajanus cajana and Pongamia glabra in pot culture. However, poor growth of sandal with A. indica is due to its dense crown and lower water-use efficiency, and being non-leguminous in nature, it could not supply the required nitrogen (Table 2). Further, poor performance of sandal was also recorded in association with leguminous species A. lebbeck. This might be due to the fact that although A. lebbeck is able to fix atmospheric nitrogen, most of it is used by the species itself due to its fast-growing nature. The gregariousness also causes lot of shading of associated species.

Further, among the non-Leguminosae species, performance of sandalwood was found to be good with teak and coconut having good lateral roots, especially in the shallow zone, sparse crown and higher water-use efficiency helped the associated parasitic sandalwood (Table 2). Thus, the performance of sandalwood not only depends on host efficiency of mineral nutrients and water, but also on the competition for above-ground resources such as light which would be critical for growth. Our findings are in agreement with those of Rocha et al., who observed significantly higher water potential (~0.85 MPa) in sandal grown with host compared to that without host (~1.27 MPa), and higher leaf nutrient content in sandal grown with host (N 2.6%, P 0.24% and K 2.31%) compared to that without host (N 2.48%, P 0.16% and K 2.31%)

Table 1. Parasitism ecology and performance of sandalwood with different hosts under natural population in the semi-arid tropics

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Family</th>
<th>No. of associations</th>
<th>Distance from the host tree</th>
<th>Girth (cm)</th>
<th>Height (m)</th>
<th>Volume (m³)</th>
<th>No. of root suckers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia nilotica</td>
<td>Leguminosae</td>
<td>16</td>
<td>2.61 ± 0.57</td>
<td>31.44 ± 1.15</td>
<td>5.37 ± 1.63</td>
<td>0.053 ± 0.036</td>
<td>0.25 ± 0.68</td>
</tr>
<tr>
<td>Prosopis juliflora</td>
<td>Leguminosae</td>
<td>08</td>
<td>1.86 ± 0.49</td>
<td>20.19 ± 0.65</td>
<td>3.88 ± 1.09</td>
<td>0.015 ± 0.013</td>
<td>1.25 ± 0.10</td>
</tr>
<tr>
<td>Azadirachta indica</td>
<td>Meliaceae</td>
<td>13</td>
<td>1.05 ± 0.16</td>
<td>12.54 ± 0.20</td>
<td>2.54 ± 0.60</td>
<td>0.003 ± 0.003</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>Tectona grandis</td>
<td>Lamiaceae</td>
<td>12</td>
<td>1.37 ± 0.57</td>
<td>16.96 ± 0.47</td>
<td>3.08 ± 0.45</td>
<td>0.008 ± 0.005</td>
<td>2.33 ± 1.23</td>
</tr>
<tr>
<td>Cocos nucifera</td>
<td>Arecales</td>
<td>06</td>
<td>1.51 ± 0.50</td>
<td>17.40 ± 0.47</td>
<td>2.93 ± 0.76</td>
<td>0.008 ± 0.004</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>Albizia lebbeck</td>
<td>Leguminosae</td>
<td>03</td>
<td>1.23 ± 0.25</td>
<td>14.00 ± 0.22</td>
<td>2.40 ± 0.30</td>
<td>0.004 ± 0.002</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>Leucanea leucocephala</td>
<td>Leguminosae</td>
<td>05</td>
<td>1.80 ± 0.57</td>
<td>20.10 ± 0.64</td>
<td>2.82 ± 0.91</td>
<td>0.011 ± 0.008</td>
<td>1.00 ± 1.41</td>
</tr>
<tr>
<td>Inga leuconothos</td>
<td>Leguminosae</td>
<td>04</td>
<td>1.40 ± 0.47</td>
<td>14.25 ± 0.30</td>
<td>2.48 ± 1.09</td>
<td>0.005 ± 0.004</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>Cassia siamea</td>
<td>Leguminosae</td>
<td>05</td>
<td>2.20 ± 0.67</td>
<td>26.00 ± 1.10</td>
<td>4.34 ± 1.02</td>
<td>0.030 ± 0.029</td>
<td>0.60 ± 0.89</td>
</tr>
<tr>
<td>F-test</td>
<td></td>
<td></td>
<td></td>
<td>&lt;0.005</td>
<td>&lt;0.005</td>
<td>&lt;0.005</td>
<td>&lt;0.005</td>
</tr>
</tbody>
</table>
Table 2. Characteristics of host plants parasitized by sandalwood under natural population in the semi-arid tropics

<table>
<thead>
<tr>
<th>Host species</th>
<th>Family</th>
<th>Effective formulation of nodulation</th>
<th>Characteristics of species</th>
<th>Water-use efficiency of trees (kg/cm)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. nilotica</td>
<td>Leguminosae</td>
<td>Present (specificity to rhizobium)</td>
<td>Extensive later roots, sparse crown, slow-growing nature</td>
<td>45.00*</td>
</tr>
<tr>
<td>P. juliflora</td>
<td>Leguminosae</td>
<td>Present (specificity to rhizobium)</td>
<td>Exotic and fast growing, sparse crown</td>
<td>37.60*</td>
</tr>
<tr>
<td>A. indica</td>
<td>Meliaceae</td>
<td>Absent</td>
<td>Dense crown, slow growing</td>
<td>13.70*</td>
</tr>
<tr>
<td>T. grandis</td>
<td>Lamiaceae</td>
<td>Absent</td>
<td>Deciduous, fast growing, sparse crown and high water requirement</td>
<td>Not found</td>
</tr>
<tr>
<td>C. nucifera</td>
<td>Aracaceae</td>
<td>Absent</td>
<td>Sparse crown, extensive lateral root system that at depth of</td>
<td>Not found</td>
</tr>
<tr>
<td>A. lebbeck</td>
<td>Leguminosae</td>
<td>Present (non-specific to rhizobium)</td>
<td>Fast growing, smaller number of nodules and non-translocation of N to dry matter</td>
<td>Not found</td>
</tr>
<tr>
<td>L. leucochepala</td>
<td>Leguminosae</td>
<td>Present (specificity to rhizobium)</td>
<td>Exotic and extensive growth and prolific regeneration</td>
<td>Not found</td>
</tr>
<tr>
<td>I. dulce</td>
<td>Leguminosae</td>
<td>Present (specificity to rhizobium)</td>
<td>Exacting species, sparse crown</td>
<td>11.9*</td>
</tr>
<tr>
<td>C. siamea</td>
<td>Leguminosae</td>
<td>Absent</td>
<td>Extensive lateral roots and moderate crown</td>
<td>21.5*</td>
</tr>
</tbody>
</table>

*Water-use efficiency was obtained from the study conducted by Tomar et al.27 on the performance of 31 tree species and soil condition in plantations established with saline irrigation.

1.68%). Further, they reported that sandal not only depends on host for mineral nutrients, but also for maintaining its water potential. Some studies indicated better plant water status of sandal grown in association with a host21,24,25.

In this study, we also noticed occurrence of root suckers. Sandalwood produced root suckers when it did not get sufficient mineral nutrients and water, mainly resulting in self-parasitism. This might be because young roots of sandalwood root suckers form an association with roots of even small plants like grasses, thereby trying to meet the nutrients and water requirements of the mother tree. Thus sandal becomes a walking tree in search of suitable host plants for survival. This is in conformity with the results of Fox and Brand26, who observed extension of sandalwood lateral roots up to >20 m from the mother tree. However, in the present study significantly higher number of root suckers were observed in association with teak (2.33) followed by Inga dulce (2.00), whereas there were no root suckers in association with neem, albizia and coconut (Table 1). This might be due to the fact that teak is a non-leguminous species and reverse translocation of phosphorus from parasite to host plant could have occurred. Rocha et al.19 also reported reverse translocation of nutrients from parasitic sandalwood to host plants, particularly of phosphorus from sandalwood to teak to the tune of 34.89% and up to 26% in casuarina. However, in case of I. dulce, it might be due non-extensive root system and lower water use efficiency (Table 2). However, lower number of root suckers in association with neem and albizia may be attributed to dense crown and non-nodulation characteristics, whereas in case of coconut it may be because of extensive lateral root system, wherein sandal might have been associated with lateral roots in multiple ways.

The present study indicates that the performance of sandalwood depends on the host characteristics such as formation of nodulation (leguminous), thin and watery lateral root system, sparse crown, slow-growing nature, translocation of nutrients, sap flow of xylem tissue and higher water use efficiency. Further, the influence of distance of association between parasite and host on the growth of sandalwood has been observed. The distance of association between parasite and host eliminates competition for above-ground resources, especially light. Hence, while establishing commercial sandalwood plantations, one should select the best host and with suitable planting geometry in order to reduce above-ground competition for its growth, one can even avoid formation of root suckers.

A. nilotica was found to be the best host among tree species followed by C. siamea. Better growth of sandalwood occurred when the distance of association was about 2.6 m away from the host (Figure 1). Hence, in the
semi-arid tropics, sandalwood cultivation could be taken up either with *A. nilotica* or *C. siamea* as the host at a planting geometry of 6 m × 6 m or 5 m × 5 m with sandalwood in the centre at 3 or 2.5 m respectively, between the host plants. Few studies suggested the effectiveness of planting sandalwood at 2.5 m within the row of host plants planted at 4 m × 5 m; sandalwood planting at 6 m × 3 m spacing with amla (*Phyllanthus emblica*) as host at the same spacing in quincunx method of planting with density of 555 plants/ha each and sandalwood planting at 4 m × 4 m spacing with casuarina as host at the same spacing in quincunx method of planting with density of 625 plants/ha each.


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